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THE DEVELOPMENT AND FUNCTION OF THE CELL PLATE IN HIGHER PLANTS.

H. G. TIMBERLAKE.

(WITH PLATES VIII AND IX)

(*Concluded from p. 99*)

2. *The genetic stage.*

THE origin of the cell plate elements occurs in the equator of the central spindle. In the onion this brings them in the midst of the carbohydrate zone (*figs. 18, 19*). There seems to be no doubt that they are thickenings of the spindle fibers. In the onion, while they are often very difficult to distinguish at first, owing to the fineness of the fibers and the abundance of carbohydrate material, it can be determined clearly that they are swellings of the fibers (*fig. 29*). There is nothing to suggest the movement of cytoplasmic granules toward the equatorial plane to form the cell plate in the manner described by Treub. Working on living cells, Treub might easily have failed to see the beginning of the cell plate. His statement that it first appears as a fine line would indicate this. The same explanation would apply to the observations of Zacharias, although it is to be noted that Zacharias described special bodies as cell plate elements and not mere undifferentiated cytoplasmic granules such as those of Treub. It is to be doubted, however, whether these bodies have any connection with a cell plate. I do not think it unreasonable to suppose that what Zacharias saw was a substance destined for the formation of the cell wall instead of a cell plate. He may possibly have seen the hyaline spaces between the spindle fibers which I have found stained orange, as above described.[36] The origin of the cell plate elements is shown more clearly in the larch. Here the thickenings are much more pronounced, being elongated bodies instead of small nodules (*figs. 4, 27c*). In this case it looks as if the activity of a fiber previously described as beginning near either daughter nucleus and going toward the equator, has become localized at the latter point, producing a swelling on the fiber. The production of such a swelling is accompanied by the further shortening of the fiber (*fig. 27c*), showing that there has been an actual transformation of the substance of the fiber in the formation of the cell plate element. While the above described process seems to agree with the older observations of Strasburger that the substance of the cell plate elements has flowed in the fibers to the equator,[37] it should be noted that there is nothing in the process I have described to indicate a collection of smaller granules within the fiber, but that the fiber itself has changed. The whole process seems to indicate a somewhat plastic character of the fiber.

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[36] *Cf.* FARMER, p. 78 of this paper.

The time relative to other phases of mitosis at which the cell plate elements occur seems to vary in the onion and the larch. In the former their appearance is concurrent with or closely following that of the carbohydrate material. The chromosomes have begun at this time to form slightly denser masses, preparatory to the reconstruction of the daughter nuclei, but separate chromosomes may still be distinguished. In the larch, the process of reconstruction goes so far before the cell plate elements appear that the daughter nuclei are often clearly outlined (*figs. 3, 4*). Whether this difference has any special significance, I cannot say. It would be interesting to compare a wider variety of forms in this respect.

As soon as the elements can be detected, they seem to form a layer throughout the thickness of the original spindle, indicating that they are simultaneous in their origin. Very early stages may have escaped observation, however, although a careful search was made for them. That such a progressive formation might be the case would be suggested by such figures as *5* and *6*, where there are some peripheral fibers on which cell plate elements have not yet formed. On the other hand, it is probable that all the fibers showing cell plate elements in *fig. 4* are the original connecting fibers, while the peripheral fibers are the previously described radiating fibers. I have previously shown that the changes in the connecting fibers, before the formation of the cell plate elements take place in all of the fibers at the same time, while the radiating fibers have apparently so changed as to form peripheral connecting fibers. Whether all of the connecting fibers form cell plate elements was a point that I could not settle with certainty. It is possible that those connecting fibers which did not show the changes described in the preliminary stages do not form cell plate elements. The phenomena observed in later stages render such a possibility more probable.

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[37] *Cf.* p. 75 of this paper.

After they first become visible, the cell plate elements continue to enlarge in their equatorial diameter until they come into contact with one another and fuse into a continuous plate. This process is accompanied by the further shortening of the fibers. In connection with the shortening of the spindle fibers there is a continued appearance of trophoplasm in the terminal parts of the spindle (*figs. 4, 5*).

The result of the processes just described may be briefly summed up as follows. There is in the spindle a young cell plate formed simultaneously from the substance of the spindle fibers. In the onion it lies in the midst of a zone of reserve carbohydrate material to be used in the formation of the new cellulose wall. In the larch such a zone is not seen at this stage. The cell plate may now be said to begin the next stage in its development.

3. *The growing stage.*

This stage is marked by the following phenomena: The central fibers continue to shorten, adding their substance to the cell plate until they have finally disappeared. The peripheral fibers begin to appear more and more bent and to form cell plate elements. As the central fibers disappear their place is partly taken by granular trophoplasm and the daughter nuclei come to lie nearer the young cell plate. While the peripheral growth is continuing, the older portion of the cell plate splits and the new wall is laid down between the halves. These processes continue until division is complete. During the period of growth the cell plate may so shift its position as to lie in a plane different from that in which it was first formed.

I have thought it best to describe the above processes separately. The fate of the spindle fibers is a question of much interest here. From the phenomena that I have been able to observe in the cells studied, I have become convinced that all of the fibers that form cell plate elements are completely used up in the growth of the cell plate. A comparison of *figs. 4, 5, 6*, and *7* is instructive on this point. In *fig. 4* the cell plate elements have just formed, the connecting fibers have drawn away from the daughter nuclei, and granular trophoplasm has appeared among the ends of the fibers of the central spindle. In *fig. 5* the cell plate elements have fused into a cell plate, the fibers have shortened still further, and the trophoplasm appears as before. *Fig. 6* is especially important. Here the fibers have become very short and the ends furthest away from the cell plates are no longer surrounded by the granular trophoplasm. These ends appear to be sharp pointed, while the portion of each fiber that is in connection with the cell plate is relatively thick. At a later stage the trophoplasm becomes distributed more throughout the region originally occupied by the central spindle. Here it frequently appears in irregular rows of granules (*fig. 7*). In this latter figure very small portions of the spindle fibers may be seen. They show the typical pointed structure above described and are distinct from the rows of trophoplasm. Throughout all of the processes involved in the formation of the cell plate the spindle fibers and the cell plate itself stain strongly with the violet of the triple stain. I have not observed the gradual transition from the violet to the orange color described by Strasburger[38] for the spindle fibers at the time when the cell plate is formed. Not only do the spindle fibers and the cell plate stain violet, but the plasma membrane of the

[38] Zellhäute.

mother cell frequently shows the same color. To be sure some preparations show the orange color in connection with the cell plate, but the violet of the cell plate itself could nearly always be distinguished. The orange color is probably due to the small amount of carbohydrate material that sometimes appears at this stage. I do not think that the presence of the above mentioned irregular rows of granular trophoplasm is to be taken as evidence that the spindle fibers break up into granular cytoplasm. My preparations show clearly that the spindle fibers are entirely distinct from these rows. The history of the fibers seems to consist of a gradual shortening and thickening until their whole substance is transformed into a cell plate, *i. e.*, a membrane. While the above description will apply to those fibers which take part in the formation of the cell plate, the fate of those radiating fibers which have no part in this process remains unaccounted for. My observations upon this latter point have been too limited to base any conclusions upon them. In a very early stage in the formation of the cell plate these fibers often seem to lose their characteristic radial arrangement and to become more of a tangled mass in the cytoplasm (*figs. 3, 4*). It is possible that they become separated from the daughter nuclei and are finally absorbed into the rest of the protoplasm. There is one other interesting case to be noted. In some cells of the larch and some of the cells of the root tip of Fritillaria, after the cell plate was formed, a few clearly defined fibers were observed in the region between each daughter nucleus and the cell plate. These fibers are probably the same that have been mentioned previously as not showing the stages preparatory to the formation of the cell plate. Their fate was not determined. *Fig. 10* is interesting in this connection. It represents a late stage in the division of the pollen mother cell when the permanent cell plates are complete, but when there still exist numerous fibers all around each nucleus, extending into the cytoplasm and reaching in many cases to the plasma membrane. Whether these are a part of the connecting and radiating fibers that existed during the earlier stages, or new fibers that have been formed after the division was complete, I did not determine. If the former supposition is true there would seem to be an unusually large number of spindle fibers which took no part in the formation of the cell plate. From the fact that in all cases observed of the formation of the first cell plate no such abundance of regularly arranged fibers was evident, I think it probable that these are mostly new fibers. Connecting stages, however, may have been overlooked. Their significance in either case is not clear. It may be that they build a new plasma membrane around each pollen grain inside of the plasma membrane of the special mother cell. Further investigation upon these late stages of the formation of the pollen grains is desirable.

The process by which the cell plate grows in area is difficult to determine with certainty. By comparing stages represented in *figs. 4–7*, I have concluded that a part of the growth of the cell plate takes place by means of the continued addition to it of the substance of the original fibers until they are entirely used up. I have already described what seems to be the process through which the fibers go in the formation of the cell plate. I consider the evidence for the complete transformation of at least part of the fibers into the cell plate conclusive. The most reasonable interpretation of *fig. 6* seems to me to be that all of the very short fibers here shown are the remains of the connecting spindle fibers shown in *fig. 4*. This interpretation is further strengthened by an examination of an intermediate stage (*fig. 5*). Here the fibers are not much shorter relatively than they are in *fig. 4*, but it is noteworthy that they are further apart, while the cell plate is, of course, more conspicuous. These facts point to the conclusion that the substance of the fibers, collecting in the middle, has simply pushed the fibers further apart, a process that constitutes the growth of the cell plate. While such a simple mechanical process may account for a portion of the growth of the cell plate, there are phenomena which seem to indicate that other processes accompany it. In all of the above figures, while there is a large area throughout in which the cell plate is in the same stage of development, it will be noted that the peripheral portions show earlier stages, and that there are fibers connected with this latter portion whose substance has not yet been used in the formation of the cell plate. In many cells these fibers show all gradations from very short ones toward the center of the cell to those reaching nearly, if not quite, to the daughter nuclei (*fig. 30*). Some of the latter, instead of extending from one nucleus to the other, extend simply from the nucleus into the cytoplasm of the opposite daughter cell. These facts would indicate that these peripheral fibers are radiating fibers which are taking part in the formation of the cell plate. The fact that the peripheral fibers appear to be more numerous and in a more compact layer in the stages represented by *figs. 6* and *7* than in earlier stages (*fig. 5*) may be explained by the crowding produced by the growth of the cell plate by the transformation of the inner fibers in the fashion described above, *i. e.*, the peripheral fibers in *fig. 6* would represent all of the radiating fibers between the boundary of the cell plate in this figure and its boundary when it had reached a stage such as that shown in *fig. 5*. The appearance of shorter fibers on the inside of the peripheral bundles and longer ones on the outside shows that the process of cell plate formation goes on gradually in these fibers from the inside outward. This is shown farther by the fact that the cell plate elements of the inner fibers have already fused into a cell plate, while the intermediate ones are often distinct, and the outer fibers often show no cell plate elements (*fig. 30*). The foregoing observations seem to show that the increase in area of the cell plate is due to a twofold process consisting (1) of a continuous transformation of the substance of the original connecting fibers, resulting in the expansion of the portion of the plate around each fiber and the consequent wider separation of the fibers; (2) concurrent with the above method occurs the addition of new cell plate elements to the peripheral portions of the cell plate, and their growth in the same fashion as those previously formed. These latter processes go on in the radiating fibers which have come into such a relation to the central spindle as to continue the first process of growth.

Another question of importance in this connection is, does the growth in area of the cell plate depend entirely upon the fibers already existing, or are new peripheral fibers formed? So far as my observations upon the larch go, I think it probable that there is no formation of new fibers, but that the whole growth takes place as a result of the changes in the existing fibers; yet the evidence on this point was not conclusive. If the hypothesis is true, whether the mother cell divides into the four cells which form the pollen grains by successive or by simultaneous division depends upon the number of spindle fibers existing in connection with the first nuclear division. If there are enough fibers to form a cell plate completely across the cell, successive division results, while if the cell plate does not reach across the cell it is absorbed into the rest of the protoplasm, and the final division takes place simultaneously after the second nuclear division. In the onion the conditions are such as to indicate the necessity for the formation of new peripheral fibers. It will be remembered that at the time of the formation of the young cell plate there were but few radiating fibers visible, and those that could be seen were relatively short, with the exception of a few near the periphery of the central spindle. In the later stages, after the fibers had entirely disappeared from the central area, the same relations of spindle fibers in the peripheral portion of the spindle could be distinguished that have been previously described in the larch (*fig. 30*). This relation indicates that there has occurred a growth at least of the original radiating fibers, with the probable production of new ones.

There is another point of importance here. The fact that some of the longer peripheral fibers may be traced to the nucleus indicates a continuous production of new peripheral fibers from the nucleus as a center. The difference, then, between the larch and the onion is possibly as follows: in the former the extent of growth of the cell plate depends upon the number of existing fibers, while in the latter, where there is necessity for the formation of a complete cell plate, the original fibers may be supplemented by the growth of new peripheral fibers. The cases in the larch in which the cell plate is not completed after the first nuclear division are possibly accounted for by the fact that the nucleus has begun to prepare for its second division, and consequently new fibers necessary for the completion of the cell plate are not produced.

Concurrent with the growth of the cell plate in extent and the disappearance of the fibers from a central portion of the spindle the nuclei come to lie nearer the cell plate (*figs. 6, 11*). This phenomenon has often been observed, but no adequate explanation for it has been suggested. From the appearance of the whole cell in the larch it would seem that such a migration of the nuclei is due to the mechanical pressure of the surrounding cytoplasm. While some granular cytoplasm has entered the region occupied by the spindle during the early stages, the later stages show very little addition until the cell plate is nearly complete and all of the spindle fibers have been nearly used up. The fibers seem to form a barrier against its ingress, so that it forms a denser layer around the whole spindle (*fig. 7*). It is possible, too, that the growth of the cell plate by the method previously described has displaced the cytoplasm around the spindle, and that such a displacement results in a greater pressure upon the nuclei.

The history of the carbohydrate material during the growth of the cell plate could not be followed with certainty. I find that it always appears plainly in connection with the spindle fibers which are forming the cell plate. In the older portions of the cell plate, however, where the spindle fibers had entirely disappeared, this substance was often indistinguishable, but in those cases where the cell plate was split, a young cell wall could nearly always be detected. It did not extend, so far as could be seen, the entire length of the cleft, but was only in the older portions (*fig. 31*). A peculiar case was sometimes found in the larch, where an incomplete cell plate appeared with a conspicuous cell wall formed between the halves of the older portion lying in the cytoplasm, with some of the original fibers still attached to it while the daughter nuclei were again dividing. Whether this cell plate and wall were finally completed, I did not determine. The same stage of development of the cell plate was often observed, in which no cell wall could be detected. The significance of the presence of a cell wall without the previous appearance of the carbohydrate material has already been discussed.

The evidence for the splitting of the cell plate before the formation of the new cell wall need not be discussed in detail here. Treub, in his experiments upon living cells, showed that the splitting occurs, and the new wall is laid down between the separated halves before the cell plate has attained its full growth. My own observations confirm this fact (*figs. 19, 31*). But one point of difference should be noted between Treub's observations and mine. In Treub's figures the beginning of the process is represented on one side of the cell where the cell plate has reached the membrane of the mother cell, while in my preparations it may be clearly seen that the splitting begins in the central region of the plate and extends toward the periphery. The mechanics of such splitting is hard to explain. The fact that no evidence of it was found except where the spindle fibers had disappeared would indicate that the fibers have no part in the process. From his observations on Fucus, where the granules which form the cell plate divide before fusion, Strasburger suggested that the splitting may be the result of a similar process in the higher plants, *i. e.*, the separate cell plate elements may divide before they fuse. If such a division takes place the two parts remain so close together that no evidence of it appears until a much later stage. Where the cell plate elements are so conspicuous as they are in the larch, it is reasonable to expect to find stages showing their division if it really occurs. The lack of such stages seems to me to indicate that the division comes later, after the elements have fused into a continuous plate. If this be true, the problem is that of the splitting of a continuous protoplasmic membrane. Strasburger decided that there is no change of a middle layer in the cell plate into a cell wall. This conclusion rests mainly upon the fact that the halves of the cell plate which appear after splitting are together equal in thickness to the original plate, *i. e.*, there has been no diminution of the substance of the cell plate during the process of splitting. That the cell wall is not a differentiated portion of the cell plate seems to me to be further shown by those cases in which portions of the separate halves of the cell plate appear with no cell wall between them (*figs. 30, 31*).

The splitting seems to be due primarily to a differentiation of the substance of the plate itself into two layers. Of what this differentiation consists is by no means apparent. It is hard to conceive of a layer of protoplasm becoming differentiated into two separate layers similar in all apparent respects to each other. To be sure, the two layers form the boundaries of separate cells, a fact which may be taken to indicate a possible chemical difference between them. This differentiation, in itself, moreover, would not account for the separation of the halves of the plate. A possible explanation for this latter phenomenon may be that there is secreted between the halves some non-stainable substance, perhaps cell sap, which serves to separate them. The apparent disappearance of the carbohydrate material before the cell plate halves appear separated may mean that there is a change in this substance, preparatory to its being deposited as a wall, of such a character that it does not take the same stain as before. It may be that it simply forms a less dense solution, and that in this form it is first deposited between the halves of the cell plate. The appearance of a stained wall would then mean that the substance had again become dense enough to take the stain. While the above explanations are purely hypothetical, I cannot see that they in any manner do violence to the observed facts. They are suggested only in order to help bring out some phases of the problem to be solved. It should be noted in this connection that the splitting of the cell plate is apparently not quite analogous to the longitudinal splitting of the chromatin thread, unless Strasburger's view that the granules divide before they fuse into a cell plate is to be accepted. In the splitting of the chromatin thread we may easily imagine the process taking place by constriction, but in the case of a continuous layer of protoplasm like the cell plate such a process would be impossible. The more so when we remember, as my figures show, that the splitting begins in the central portion and extends outward.

The change in position of the cell plate during its growth is shown by *figs. 12* and *21*. The explanation of such a change is not obvious. The figures show that the nuclei do not move with the cell plate. Whether the cell plate ever changes from a true diagonal to a transverse plane I was unable to determine. The figures show only those cases where the plane in which the cell plate was first formed was not a true diagonal. Nemec[39] has shown that the position and form of the young spindle can be determined to some extent by means of pressure or tension exerted upon the tissues in which the dividing cells occur. It is possible in these cases that the conditions of pressure or tension upon the single cells have so changed by growth of some of the surrounding cells of the tissue as to bring about the change in position of the cell plate. The most obvious significance of the shifting of the cell plate is that the original position of the spindle cannot always be taken to determine accurately the ultimate plane of division of the cell.

CONCLUSIONS.

1. The most obvious and at the same time most important conclusion to be derived from the foregoing observations is that the division of the cell body is due to the activity of the kinoplasm of the cell. The splitting of the cell plate, or at least its differentiation into separate layers, is in the higher plants the essential act in the division of the cell body, for it is not until such a differentiation has taken place that there is a separation of the protoplasm of the mother cell into two distinct parts. That the cell plate is kinoplasmic has already been

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[39] Ueber Kern u. Zelltheilung bei *Solanum tuberosum*. Flora **86**: 214. 1899.

insisted upon by Strasburger in two of his recent papers.[40] The difference between Strasburger's observations and mine is that in the former only a small portion of any one fiber is used in the process of cell plate formation, while in the latter the substance of the whole fiber becomes transformed into a portion of the cell plate, *i. e.*, in the one case the cell plate is simply a product of the activity of the kinoplasmic fibers, the fibers themselves not being used in the process, while in the other case the cell plate is a result of a change of form of the substance composing the fibers. The identity in character of the substance of the cell plate and that of the spindle fibers has an important bearing on the relations of the different methods of cell division occurring in different groups of plants. The process of free cell formation in the embryo of Ephedra, as described by Strasburger, is an interesting case of kinoplasmic activity, in which the division takes place around a single nucleus instead of between two nuclei as in regular cell division. The fact that the membranes are formed simultaneously would show that this process goes on around all parts of the nucleus alike. It might be contrasted in this respect with the formation of ascospores, as described by Harper, in which the growth of the membrane is a progressive one and the nucleus is consequently modified in form to suit the necessity of kinoplasmic activity from one point alone. The method of division of the egg from the endosperm mother cell and the synergids, as described by Mottier[41], presents a process intermediate between the method of free cell formation in Ephedra and that of regular cell division. Here, where there are two nuclei lying adjacent to one another, the cell plate is formed in connecting spindles between them, but where, as in the case of one synergid in Mottier's *fig. 22*, the fibers end blindly in the cytoplasm, a cell plate is formed in such fibers, following the method of Ephedra. In all of the above cases the formation of a membrane from the fibers is an established fact. The method of cell division by constriction of the plasma membrane, which occurs in many filamentous algæ, may be analogous to the growth of the plasma membrane as the cell increases in size, with the difference that in the former case the growth of the plasma membrane is localized and proceeds without the accompanying growth of the cell contents.

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[40] Ueber Cytoplasmastructur und Zellhäute.

[41] Ueber das Verhalten der Kerne bei der Entwickelung des Embryosacks und der Vorgänge bei der Befruchtung. Jahrb. f. wissen. Bot. **31** : 123. 1898.

2. I have already indicated what seems to me to be the relation of the nucleus to the kinoplasm in the process of cell division. It is the center of the metabolic processes concerned in the production of the kinoplasm. Whether there is a transformation of some previously existing substance of the cell into the filar form of kinoplasm I have not been able to determine. From the two facts that no such transformation is visible and that a great many of the fibers are used up in the formation of a membrane, I think it probable that they are formed anew in each cell. That the chromatin is the real center for their formation is shown by the formation of new radiating fibers around the daughter nuclei in the onion during the diaster stage, and by the formation of a spindle around a single chromosome in the manner described by Juel for Hemerocallis. The history of the kinoplasm in a single cell of the higher plants would seem to be as follows. It is formed as fibers around the nucleus as a center. In this form the kinoplasm takes part in the process of nuclear division, and later divides the cell by a part of the fibers being transformed into a membrane which becomes in splitting the plasma membranes of the daughter cells.

In cases where cell division does not follow immediately upon nuclear division the filarplasm may be absorbed into the general protoplasm of the cell, either to reappear or to be formed anew when needed for cell division. The ultimate form of the kinoplasm of any one cell seems to be reached when it has become a plasma membrane. It is then concerned with the activities of the resting cell. The transformation of kinoplasm from the filar into the membrane form seems to show that the hypothesis of a permanent substance, which may be described by the term "filarplasm," lately proposed by Strasburger,[42] is not well founded. To be sure there are, in a great many cells, spindle fibers that seem to take no part directly in the formation of membranes, but they apparently lose their filar form. The most permanent form of the kinoplasm seems to be of the membrane. It would seem better, then, to retain the older physiological term kinoplasm, since such a term would denote a substance having certain physiological properties without necessarily being limited to any one form. The conclusion reached by Kostanecki[43] of the permanency of the spindle fibers in the cell, and that they are always reproduced by division of the individual fibers, "omnis radius e radio," is, as Nemec[44] has pointed out, unsupported by the history of the fibers in plant cells. It would be impossible, moreover, to account thus for the manner in which the fibers are transformed into a membrane.

3. The relation of the carbohydrate material to the process of division would seem to show, as already stated, that the substance for the formation of the cell wall is held in a reserve form in the protoplasm before it is actually needed for the process of wall formation. The fact that it appears in connection with the spindle would suggest, as Farmer and Williams have shown, that the spindle fibers have for their substance a conductive function. These authors did not ascribe a formative function to the fibers because they did not find any cell plate. It is not impossible that the cell plate may have been entirely overlooked in this case. In some of my own preparations it was often very difficult to discover the young cell plate in the midst of the carbohydrate material.

If the above mentioned relation of the carbohydrate material to the spindle be taken in connection with the facts shown by Klebs,[45] and by Townsend,[46] that the presence of a nucleus is necessary for the formation of a cell wall, there would be some evidence for the hypothesis that the nucleus forms the cell wall substance.

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[42] Zellhäute. [43] *Op. cit.* [44] Kerntheilung von *Allium Cepa*, 321.

[45] Beiträge zur Physiologie der Pflanzenzelle. Untersuch. a. d. botan. Institut z. Tübingen **2** : 500. 1888.

[46] Der Einfluss des Zellkerns auf Bildung der Zellhäute. Jahr. f. wissen. Bot. **30** : 484. 1897.

The investigations described in the foregoing pages were begun at Lake Forest University under the direction of Professor R. A. Harper, whose helpful interest and valuable criticism have continued throughout their progress. The work was continued and practically completed in the botanical laboratory of the University of Michigan during the years 1897–8 and 1898–9. I wish here to thank Professors Spalding and Newcombe of the above laboratory for the liberal way in which material and equipment were provided, and for many helpful suggestions received. Professor Jacob Rheigard, of the department of zoölogy of the University of Michigan, very kindly allowed the use of the photographic apparatus of that department, and Dr. J. B. Johnston aided me greatly in making the photographs.

THE UNIVERSITY OF WISCONSIN.

EXPLANATION OF PLATES VIII AND IX.

Figs. 1–21 are reproductions of photographs made with the Zeiss photomicrographic apparatus. (Figs. 9 and 22 have been purposely omitted.) Figs. 23–31 are from drawings made with the aid of the camera lucida, Zeiss 2^{mm} immersion objective, and compensation oculars 8, 12, and 18. The size has been reduced $\frac{1}{5}$ in reproduction.

Figs. 1–10. *Larix;* pollen mother cells.

FIG. 1. Equatorial plate. × 750.

FIG. 2. Early diaster showing first stages in preparation for cell plate formation; the central spindle is differentiated into three zones. × 1200.

FIG. 3. Later than preceding; central spindle alike throughout. × 1200.

FIG. 4. Cell plate elements just forming. × 1200.

FIG. 5. Young cell plate has begun to grow in area; connecting fibers are beginning to disappear. × 1200.

FIGS. 6–10. Later stages in the growth of the cell plate; see explanation in text. × 1200.

FIGS. 11–21. *Allium Cepa;* cell of growing root-tip.

FIG. 13. Equatorial plate; spindle fibers arranged into strands or bundles. × 1500.

FIGS. 14–15. Metaphases showing granular appearance of region between the groups of daughter chromosomes. × 1500.

FIG. 16. Stage corresponding to *fig. 2*. × 1500.

FIGS. 17–19. Later stages showing the equatorial zone containing carbohydrate material. × 1500.

FIGS. 18–19. Formation of cell plate in the midst of the zone of carbohydrate material. × 1500.

FIGS. 20 and 21. Growth of cell plate and disappearance of spindle fibers. × 1500. See also *fig. 11*.

FIGS. 12 and 21. Stages showing change of position of cell plate from a diagonal to a transverse position. × 1500.

FIG. 23. *Larix;* showing arrangement of spindle fibers and differentiation of cytoplasm into layers. × 3000.

FIG. 24. *Larix;* details in relation of radiating fibers to the connecting fibers in a stage represented by *fig. 3*. × 4500.

FIG. 25. *Allium;* portion of spindle in late metakinesis, showing relations of fibers to one another and distribution of granules in the spindle. × 4500.

FIG. 26. *Larix;* two radiating fibers lying adjacent to the central spindle and crossing in such a way as to appear fused. × 4500.

FIG. 27. *Larix;* different stages in the transformation of the substance of a spindle fiber into a portion of the cell plate. × 4500.

FIG. 28. *Allium;* relation of the connecting fiber to the carbohydrate material at the equator. × 3000.

FIG. 29. *Allium;* cell plate elements formed on the connecting fibers in the midst of the carbohydrate material. × 3000.

FIG. 30. *Allium;* late stage in the growth of the cell plate, showing the relation of the outer radiating fibers to the growing portion of the plate. × 4500.

FIG. 31. *Allium;* cell plate with young cell wall showing in the cleft where the cell plate is split. × 3000.

ERRATUM: on p. 85, line 16 from top, *fig. 10* should read *fig. 13*.